

**SUBFAMILIES OF CACTACEAE JUSS., INCLUDING  
BLOSSFELDIOIDEAE SUBFAM. NOV.**

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**ABSTRACT**

New data from chloroplast DNA comparisons reveal *Blossfeldia* Werd. (Cactaceae) as an isolated lineage between a basal grade of subfamilies Opuntioideae-Pereskioideae-Maihueñoideae and a more derived sister pair of clades, making recognition of a new subfamily warranted. Based on parsimony and Bayesian cladistic analyses of chloroplast DNA sequences reported elsewhere, as well as morphological distinctiveness, **Blossfeldioideae** Crozier subfam. nov. is erected and Rhipsalidoideae Burnett is resurrected. An abbreviated history of suprageneric classification in the family and a key to the six subfamilies of Cactaceae recognized here is provided.

**KEY WORDS:** *Blossfeldia*, Blossfeldioideae, Maihueñoideae, Opuntioideae, Pereskioideae, Rhipsalidoideae, Cactaceae.

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As in many other families of flowering plants, there has been little unanimity in the suprageneric classification of the Cactaceae Juss. but slowly the discovery of new taxa, careful morphological observation, and other contributions to phylogenetic knowledge have led to refinements. The Cactaceae (Cacti) of Jussieu (1789) encompassed all the known cacti of the time under the single genus *Cactus* L., but also included *Ribes* L. (Grossulariaceae). Apparently aware of studies by de Candolle (1828) and Lindley (1830) that excluded Grossulariaceae from Cactaceae, Eaton (1836) nonetheless chose to divide Jussieu's Cactaceae into two subfamilies, distinguishing Cactoideae (Cactaeae) from Grossulariaeae. The Grossulariaceae were not included in Burnett's (1835) concept

of Cactaceae (Nopalaceae) divided into subfamilies Rhipsalidoideae (Rhipsalidae) including only the genus *Rhipsalis* Gaertner, and Opuntioideae (Opuntidae) including the genera *Mammillaria* Haw., *Melocactus* Link & Otto, *Echinocactus* Link & Otto, *Cereus* Mill., *Opuntia* Mill., and *Pereskia* Mill. Engelmann's (1876) creation of subfamily Pereskioideae (Peireskieae) and division of the family into three subfamilies for the *Botany of California* begins the modern era in cactus classification. Treating only a few genera Engelmann heralded the classification in three subfamilies years ahead of Schumann (1890,1898) whose Cactoideae (Cereoideae), Pereskioideae (Peireskioideae) and Opuntioideae have been included in most subsequent taxonomic studies (Berger 1926,1929; Backeberg 1958,1966; Buxbaum 1958, Barthlott and Hunt 1993; but see also Britton and Rose 1919-1923; Hunt 1967; Benson 1982 for recognition of these same groups at tribal rank). Cactoideae Eaton, Opuntioideae Burnett, and Pereskioideae Engelm. appear to be validly published, and under the International Code of Botanical Nomenclature (Greuter et al. 2000) these names take priority over the subfamilial names authored by Karl Schumann.

The Opuntioideae and Pereskioideae have been clearly circumscribed and almost uniformly recognized in modern times, discounting the uncertain placement of *Maihuenia* Schum., a genus of only two species from the southern Andes and Patagonia. First associated with the caespitose opuntias, *Maihuenia* was soon reassigned to the Pereskioideae by Schumann (1898) based on spine, flower, and seed characters. Gibson's (1977) interpretation of stem tissues and pollen features supported this placement, however Bailey (1968) excluded *Maihuenia* from the Pereskioideae based on stem and vascular anatomy, and was also unwilling to place it with Opuntioideae based on similar terete leaves. Bailey noted similarities of pollen and highly modified wood that to him suggested a possible relationship with the Cactoideae (Cereoideae). Later, the genus was raised to subfamilial rank by Fearn (1996) who may have been spurred by provisional molecular evidence (see Leuenberger 1997 p.58 and references within, Doweld 1999 p.25). With the exclusion of *Maihuenia* the monophyly of the Pereskioideae, including only *Pereskia* Mill., has never been questioned on morphological grounds.

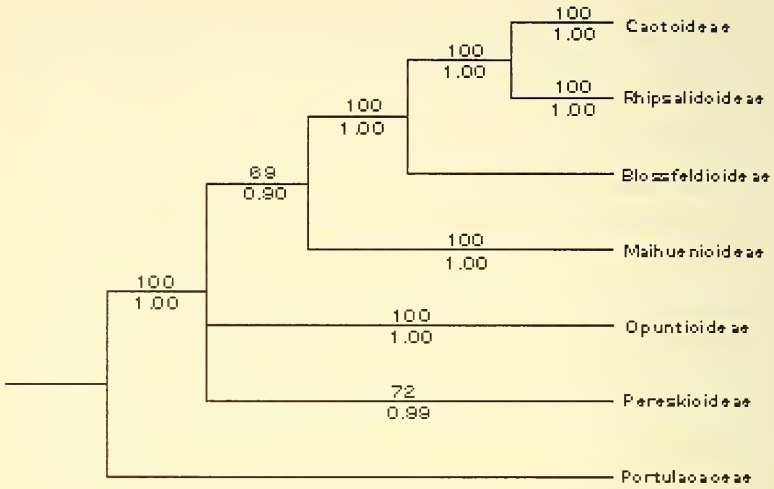


Figure 1. Relationships of Cactaceae subfamilies. Congruent topologies resulted from maximum parsimony and Bayesian phylogenetic analyses of 16,620 base pair chloroplast data set comparing 98 cactus species and 3 outgroup taxa (simplified from Crozier et al. 2004 in prep.). Bootstrap values shown above branches; Bayesian probabilities shown below. For one of the 52 most parsimonious trees the Consistency Index excluding uninformative characters = 0.48, Retention Index = 0.78.

However, the molecular study of Nyfeller (2002) was unable to support the monophyly of *Pereskia*. A broader sample of six *Pereskia* species in the study by Crozier et al. (2004 in prep.) does form a monophyletic clade with moderate bootstrap support and significant Bayesian probability (see Fig. 1). Together the *Opuntioideae*, *Pereskioideae* and *Maihuenioideae* represent less than 15% of the species of the family. The rest of the family, a morphologically diverse group of more than 1100 species (Hunt 1999), has traditionally been lumped into the single subfamily *Cactoideae* based on the absence of synapomorphies defining the *Pereskioideae* and *Opuntioideae*. This diversity has usually been subdivided into 8 or 9 tribes (see Barthlott 1988 for a review; Barthlott and Hunt 1993). However, comparative analyses of chloroplast DNA

sequence data now provide statistically well-supported evidence of two distinct major lineages. The name Rhipsalidoideae Burnett can be used to recognize the clade containing most columnar cacti, epiphytes, and globular cacti of South America (see Fig. 1).

Molecular studies are rapidly increasing our recognition of monophyletic lineages in the Cactaceae facilitating improved classification that reflects evolutionary relationships. Results of parsimony analysis of more than 6,000 base pairs of chloroplast DNA sampled from 120 representative taxa across the family first revealed *Blossfeldia* as a monophyletic lineage sister to the Cactoideae-Rhipsalidoideae clade with strong bootstrap support (Crozier and Jansen, 2001). Nyfeller (2002) independently inferred the same position of *Blossfeldia* rejecting the possibility that this might be a taxon-sampling artifact (long-branch attraction) in parsimony and maximum likelihood combined analysis of trnK-matK and trnL-trnF data. Crozier et al. (2004 in prep.) compared 98 species of cacti, and outgroups from the Portulacaceae and Didieraceae for 16,620 base pairs of chloroplast data using parsimony analysis that yielded strong bootstrap support for the Blossfeldioideae as well (see Fig. 1.). Furthermore, statistical support for this relationship of *Blossfeldia* was 100% probable in a Bayesian analysis run for 4 million generations of that combined data set representing 13 functional regions of the chloroplast, including genes, introns and intergenic spacer regions. In addition, *Blossfeldia* shares with the Pereskioideae, Opuntioideae and Maihueñoideae unique chloroplast DNA motifs in multiple markers (Crozier et al., 2004 in prep.). For this reason and its distinctive morphology I am proposing to place *Blossfeldia* in its own subfamily.

**Blossfeldioideae Crozier, subfam. nov.**

Type: *Blossfeldia* Werd., Kakteenkunde 11:162 (1937).

Monotypic (1 species). Type species: *B. liliputana* Werd.

*Caudex crassus, caulis simplex dein proliferans, depresso-globosis vel disciformibus 2.5 cm diametro vel parvioribus, neque costatis neque tuberculatis vertice depressioribus lanoso, sine hypodermata epidermata una tabulato sine epicuticulo ceracea, parietibus cellularum*

*epidermis externus vix incrassatis, stomata perpauci 1 per mm<sup>2</sup>, stomata fovea areolari restrictis. Semina parva globosa strophiole fere quam grandiore quam semina gerentibus.*

Perennial herb from a fleshy taproot, succulent, poikylhydric, body swelling immediately after rainfall. Stem solitary or caespitose, individual stems obpyriform when hydrated or flattened, disc-shaped with conspicuous central cuplike depression when desiccated, lacking ribs or pronounced tubercles, 1-1.5 (2.5) cm in diameter. Stomata restricted to areolar pits, overall density much less than 1 per mm<sup>2</sup>. Pericarpel sculptured with podaria tipped by small lanceolate to triangular scales, or with only a few scales and essentially glabrous on the lower part, bearing whitish to gray wooly hairs in the axils.. Pollen subspherical, tricolpate, with smooth exine. Fruit a juicy berry, spherical to ovoid or pyriform, about 0.5 cm across, with podaria bearing large scales, and axillary hair in small bundles, without bristles, side splitting when ripe then disintegrating over time to release the seeds. Seeds globose, small, 0.5 mm in diameter, testa minutely papillose, shiny red-brown, with large ivory hilum.

**Blossfeldiae** Crozier, **trib. nov.**

Type: *Blossfeldia* Werd., *Kakteenkunde* 11:162 (1937).

Monotypic (1 species). Type species: *B. liliputana* Werd.

*Caudex crassus, caulis simplex dein proliferans, depresso-globosis vel disciformibus 2.5 cm diametro vel parvioribus, neque costatis neque tuberculatis vertice depressioribus lanoso, sine hypodermata epidermata una tabulato sine epicuticulo ceracea, parietibus cellularum epidermis externis vix incrassatis, stomata perpauci 1 per mm<sup>2</sup>, stomata fovea areolari restrictis. Plantae aphyllae, areolis inermibus coactis. Flores solitarii axillaribus turbinatis vel infundibuliformibus 0.6-1.5 cm longis hernioploditis. Fructis globosis vel pyriformibus brumeis dehiscentibus dein fatiscentibus. Semina parva globosa strophiole fere quam grandiore quam semina gerentibus.*



Perennial herb from a fleshy taproot, succulent, poikylhydric, body swelling immediately after rainfall. Stem solitary, caespitose with age dividing dichotomously, laterally, or sprouting from rootstock exposed to light, individual stems obpyriform when hydrated or flattened disc shaped with conspicuous central cuplike depression when dessicated, lacking ribs or pronounced tubercles, 1-1.5 (2.5) cm in diameter, grey-green to dark green depending on environmental conditions. Stems with a single epidermal layer, external cell walls barely thickened, lacking epicuticular wax coating. Stomata restricted to areolar pits, overall density much less than 1 per mm<sup>2</sup>. Areoles spirally arranged, circular in face view, tomentose, unarmed. Flowers solitary, subapical arising from the depressed felted crown, usually hermaphroditic, sometimes dichogamous or even unisexual (trimonoecism), opening only in full sun. Flowers turbinate to funnellform, 0.6-1.5 cm long, sometimes with nectary glands. Pericarpel sculptured with podaria tipped by small lanceolate to triangular scales, or with only a few scales and essentially glabrous on the lower part, bearing whitish to gray wooly hairs in the axils. Perianth segments sequentially intergrading in form and color, reflexed. Outermost tepals acuminate, olive-brown. Inner tepals narrowly ovate, rounded apically, white to pale yellowish-white. Androecium in more than two series, equivalent in length. Stamen sometimes wanting, filaments whitish, anthers yellow to gold-yellow. Pollen subspherical, tricolpate, with smooth exine. Stigma and style sometimes wanting, whitish. Stigmatic branches lanceolate, tapering distally, papillose only on the inner surfaces and margins. Fruit a juicy berry, spherical to ovoid or pyriform, about 0.5 cm, wall irregularly sculptured with podaria bearing large scales, and axillary hair in small bundles, without bristles, brown, side splitting when ripe then disintegrating over time to release the seed. Seeds globose, small, 0.5 mm in diameter, testa minutely papillose, shiny red-brown, with large ivory hilum. Chromosome number:  $n = 33$  (Ross, 1981).

*Blossfeldia* lacks xeromorphic stem features of other globular cacti (Barthlott and Porembski 1996) and its globose ornamented and arillate seed is distinctive in the family. Equally distinctive is the restriction of stomata to areolar crypts and extremely low density of stomata on the

stem. Based on well supported molecular analyses this smallest member of the Cactaceae represents an isolated lineage, and appears to be the only extant transitional form between the basal grade of subfamilies Pereskioideae-Opuntioideae-Maihuenioideae and a strongly supported clade of more derived cacti (Fig. 1.). At present no other member of the Blossfeldioideae has been identified.

Whereas distinct morphologies separate subfamilies Opuntioideae, Pereskioideae, Maihuenioideae and Blossfeldioideae, the remainder of species are so morphologically diverse that phyletic subdivision of the group has been difficult because of parallel and convergent evolution in vegetative and floral morphology (Buxbaum 1958; Barthlott and Hunt 1993). Classifications have been confusing and unstable, and circumscription of suprageneric taxa continues to be modified to try to meet modern expectations of monophyly (Buxbaum 1974, Gibson and Nobel 1986; I.O.S. 1986,1990; Barthlott 1988, Barthlott and Hunt 1993). In light of recent molecular studies a review of the entire suprageneric classification of the family, at least at the subfamilial level, seems in order.

The two lineages comprising the clade sister to Blossfeldioideae are quite distinct (see Fig. 1.) and well supported by high bootstrap values and Bayesian probabilities based on the chloroplast DNA studies of Crozier et al. (2004 in prep.). These results show that the two groups are much more distantly related than are the groups of genera within each of them. It is appropriate to recognize these sister clades at equal rank. In so doing the information content of the classification is increased, and the adoption of six subfamilies is not so numerous as to negate its usefulness. Therefore, I am proposing that the proper application of the autonym Cactoideae belongs to the clade of North American globular cacti that includes *Mammillaria mammillaris* Haw., the conserved type species of the family. This clade corresponds to tribe Cacteae sensu Barthlott and Hunt (1993), though Backeberg (1966) may have been the first to recognize this monophyletic lineage with his subtribe Boreocactinae, a *nomen nudum*. The morphologically isolated position of this group from other tribes was pointed out specifically by Barthlott (1988) who

noted "Zu allen übrigen Triben können keine Beziehungen erkannt werden." The earliest valid subfamilial name applicable to the sister clade of columnar, epiphytic and South American globular cacti appears to be Rhipsalidoideae Burnett. The Rhipsalidoideae as recognized here includes all members of tribes Rhipsalideae DC., Echinocereae (Br. & Rose) Buxb., Hylocereae (Br. & Rose) Buxb., Cereae Salm-Dyck, Pachycereae Buxb., Trichocereae Buxb., Browningieae Buxb. and, with the exclusion of *Blossfeldia*, Notocacteeae Buxb.

The Cactaceae has been notorious for parallel evolution in morphology that thwarts phylogenetic classification. Parallel reduction in shoot, leaf, flower and seed development in multiple phylogenetic lineages was described by Buxbaum (1951, 1956 and 1965) following phylogenetic ideas of Berger (1926). Although abundant molecular synapomorphies distinguish the Cactoideae and Rhipsalidoideae, unique morphological synapomorphies uniting each clade are difficult to identify. A key to the six subfamilies recognized on the basis of morphological discontinuities and DNA evidence is provided below.

### KEY TO THE SUBFAMILIES OF CACTACEAE

- 1a. Areoles bearing glochids, seeds large, alveolate;  
bony aril covering the entire seed.....**Opuntioideae**
- 1b. Areoles without glochids, seeds small, usually  
exarillate or only the hilum covered by a strophiole  
or corky strophioliar pad.
  - 2a. Plants with persistent photosynthetic leaves on stems.
    - 3a. Plants tree-like or shrubs with laminar leaves...**Pereskioideae**
    - 3b. Plants low caespitose shrubs with terete leaves.....  
.....**Maihuenioideae**
  - 2b. Plants without persistent photosynthetic leaves on stems.



- 4a. Stems virtually lacking stomata except in sunken crypts; stems lacking thickened cuticle with epidermis lacking thickened outer cell walls, lacking thickened hypodermal layer, stem always flattened globular or disciform less than 25mm diameter; round seeds with strophiole nearly equal in size to the rest of the seed.....**Blossfeldioideae**
- 4b. Stems with stomata or if few then not restricted to cylindrical crypts, usually with thickened cuticle, an epidermal layer with outer cell walls thickened and a hypodermal layer; stems variously flat, triangular globular or columnar; seeds not round, seeds usually exarillate (except in *Parodia*, *Strombocactus*, and *Aztekium*).
- 5a. Flowers with naked pericarpels, bearing neither areoles nor scales.
- 6a. Plants globular or short cylindrical, never tall columnar, never with a cephalium, never epiphytic, restricted to North America or the Caribbean; seeds usually with disjunct hilum and micropyle .....**Cactoideae**
- 6b. Plants with flat (*Schlumbergera*), triangular, columnar (*Pachycereus*, *Pilosocereus*, *Espositoopsis*) stems or epiphytic (*Rhipsalis*, *Hatiora*, *Lepismium*), if globular then bearing a cephalium (*Melocactus*) or restricted to South America (*Uebelmannia*, some species of *Matucana*), seeds with conjunct hilum-micropylar region .....**Rhipsalidoideae**
- 5b. Flowers with pericarpels bearing scales and/or areoles.
- 7a. Areoles on pericarpel felted, or with hairs, bristles or spines.....**Rhipsalidoideae**

7b. Areoles on pericarpel naked.

8a. Stems columnar or epiphytic, seeds always with conjunct hilum-micropylar region, American or Caribbean.....**Rhipsalidoideae**

8b. Stems globular or short cylindrical (*Astrophytum*, *Echinocactus*, *Sclerocactus papyracantha*) or barrel shaped (*Ferocactus*, *Echinocactus*), never epiphytic, seeds usually with disjunct hilum and micropyle, restricted to North America.....**Cactoideae**

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